FISH AND AMPHIBIAN TRACE FOSSILS FROM WESTPHALIAN SEDIMENTS OF BOHEMIA

by VOJTĚCH TUREK

ABSTRACT. In the Radnice basin of Bohemia, fish and ethologically comparable amphibian ichnofossils of Upper Carboniferous (Westphalian C) age occur in limnic sediments that suggest humid, tropical conditions. Swimming trails of fish belonging to the subclass Actinopterygii, and probably to the order Palaeonisciformes, closely resemble trails in limnoglacial deposits of the Karroo Dwyka and Ecca Series in South Africa (Anderson 1970, 1976); the new trails are assigned to *Undichna radnicensis* ichnosp. nov. Footprints, swimming traces, and resting traces of labyrinthodont amphibians belonging to the order Temnospondyli (branchiosaurids or dissorophids) are associated with the fish trails. The swimming traces are assigned to *Lunichnium gracile* ichnosp. nov. and *L. anceps* ichnosp. nov., while the morphologically variable footprints are assigned to *Gracilichnium* (?) *chlupaci* ichnosp. nov.

THE swimming traces of fish and tetrapods have rarely been described. The makers of such traces are difficult to identify, even at the class level, and there are doubts as to whether some were made by vertebrates or invertebrates. The number of distinct ethological types of traces from the Carboniferous Period that can be correlated is still very small.

A recent intensive palaeobotanical investigation of the Radnice Basin (a classic region of central Europe for the limnic Carboniferous since the work of Sternberg 1820–1838) has led to the discovery of a rich trace fossil assemblage. Many traces of invertebrates, fish, and amphibians were discovered in claystones of Westphalian C age immediately underlying the Radnice seam (text-fig. 1, box 1) at an open-cast mine in Přívětice-Ovčín, west Bohemia. The amphibian traces are remarkable chiefly because it is possibile to correlate directly between swimming traces, resting traces, and walking traces (footprints). The only other ichnofossils previously described from the Radnice Member were two trails tentatively ascribed to arthropods by Walter (1982). Body fossils are also rare and, with only one or two exceptions, are all arthropods. Any determination of the trace-makers must therefore be based upon the fauna of the subjacent Nýřany Member in particular (see Fritsch 1879–1901), and of the European Permo-Carboniferous in general.

Ichnofossils were first found in the Přívětice-Ovčín locality by K. Drábek in 1983, and a preliminary report with figures of the most important specimens was given by Turek (1986). The material is well preserved. Hyporelief is always better than epirelief, but all the morphological descriptions have been related to epirelief. This paper is concerned with vertebrate trace fossils; invertebrate trace fossils will be discussed elsewhere.

REGIONAL SETTING AND STRATIGRAPHY

Rocks of Permo-Carboniferous age are distributed over central and western Bohemia, filling an intracratonic depression between ridges of the Variscan mountain range. This depression was infilled after completion of the main Variscan orogeny, in the Upper Carboniferous and Lower Permian. Upper Carboniferous sediments of continental origin occur today in a group of tectonically downthrown blocks, north-east of Plzeň; they comprise the Radnice basin. Their deposition was preceded by volcanic activity. The limnic sediments are of Westphalian age and belong to the Radnice Member of the Kladno Formation (Westphalian C).

The Přívětice-Ovčín open-cast coal mine lies in the southern part of the Radnice basin, between the villages of Přívětice, Radnice, and Skolmelno. Two worked coal seams (the lower and upper Radnice seams) are

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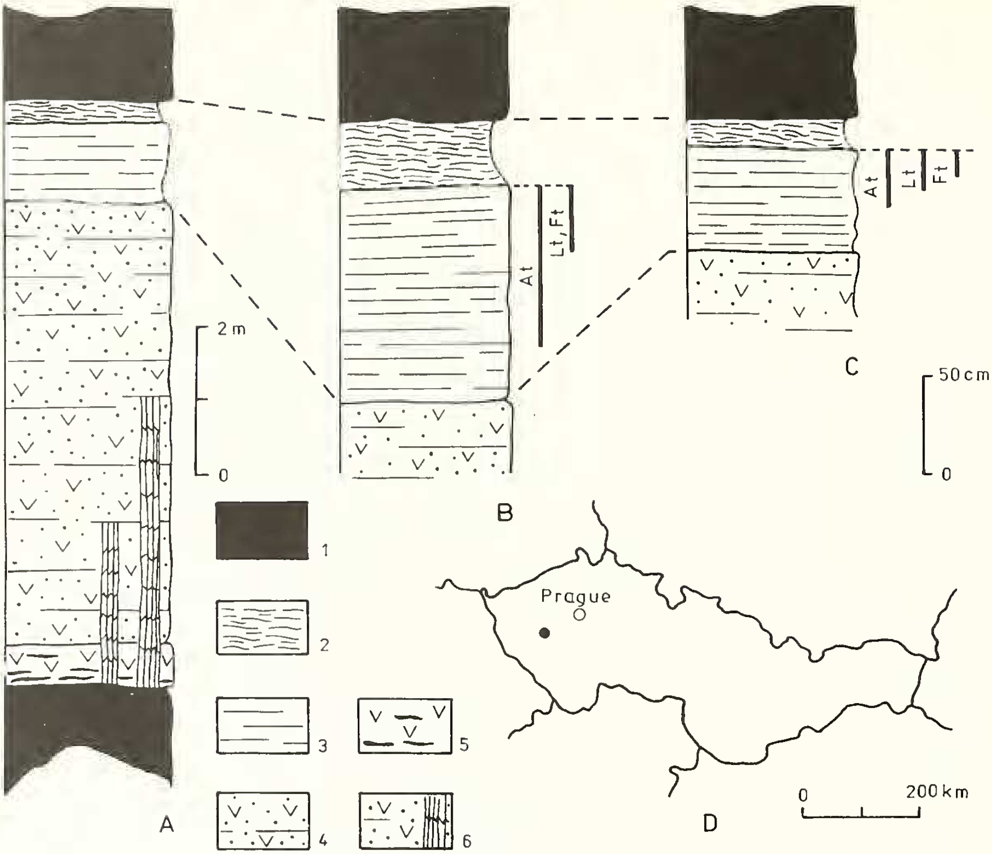


TEXT-FIG. 1. A, the Westphalian sequence exposed at Přívětice-Ovčín, Radnice basin, Czechoslovakia, showing the position of trace-bearing beds. B, C, upper part of the general sequence showing vertical distribution of ichnofossil groups in the central (B) and eastern (C) area of the outcrop. D, sketch map of Czechoslovakia showing locality (closed circle). Abbreviations: 1, coal; 2, clay; 3, claystone; 4, tuffaceous rocks (tuffaceous claystones, tuffite, tuff); 5, tuff with well-preserved plants and very rare arthropods; 6, *in situ* stems of equisetophytes, lycopodiophytes, etc.; At, arthropod traces; Lt, amphibian traces; and Ft, fish trails.

interbedded with 8–12 m of volcanic tuffs, tuffaceous claystones, and claystones (text-fig. 1). The uppermost claystones contain the ichnofauna and are grey and very fine-grained; they grade upwards into a grey clay that immediately underlies the upper Radnice seam.

Stratigraphic divisions are based primarily on the contained macroflora (Sternberg 1820–1838; Ettingshausen 1854; Feistmantel 1869; Němejc 1953; and others). The rare fauna of Westphalian age found near Radnice consists of terrestrial arthropods (Zajíc and Štamberg 1986). An isolated and undescribed find of cartilage from an unidentified fish is exceptional. Such fossils all come from a single, water-lain, tuffaceous horizon. One undescribed insect fossil was recently found in the overlying claystones.

SEDIMENTOLOGICAL REMARKS

The material filling the Radnice basin was deposited in a tropical, humid environment. Its rapid sedimentation was influenced by intensive volcanic activity. *In situ* lycopodiophytes, equisetophytes, etc., some 4–5 m tall, grow out of the lower Radnice coal seam and cross the overlying layers of tuffaceous rocks at a slight angle. The length of time during which these tuffs and tuffaceous claystones were deposited must therefore have been a matter of months, or at most, a few years. A decrease in the supply of volcanic material was undoubtedly the cause of the much slower sedimentation rate characteristic of the overlying claystones – although even this rate was very probably much higher than average for the Upper Carboniferous in central Bohemia (cf. Kukal 1984). The upper grey claystones are very fine-grained and perfectly flat-bedded, with no intrastratal bioturbation structures. The absence of bioturbation, and hence of any infauna, was probably due to a limited food supply (cf. Cohen 1984).

It is clear from the given ichnocoenosis that all traces were formed subaqueously and below wave base. Their depth range is hard to estimate, owing to the paucity of data on the size of the lake and the configuration of the surrounding area, etc. It is assumed, however, that the depth of the lake in this marginal part of the basin could not have been more than a few metres.

The absence of body fossils – apart from isolated plant remains (and discounting the appendices of lycopodiophytes which penetrated the clay from above) – is considered to result from two factors: 1, an acid reaction of the water, caused by the addition of acidic volcanic products from the area surrounding the lake (cf. Mašek 1973); and 2, efficient oxygenation of the water and hence rapid oxidation of organic matter. Indeterminate imprints may represent the carcasses of small invertebrates, although it seems likely that most such animals were devoured by amphibians and fish. The bodies of dead vertebrates floated to the surface and decomposed, and so left no identifiable traces.

OCCURRENCE OF ICHNOFOSSILS

All the ichnofossils come from the southern and south-eastern parts of the coal-bearing depression mined at Přívětice-Ovčín. Material was collected at four outcrop localities, aligned approximately south-east by north-west and spanning about 80 m. Ichnofossils were found only in the uppermost part of the interval between the lower and upper Radnice coal seams (text-fig. 1), in grey, thinly bedded to tabular claystones whose thickness rapidly diminishes eastwards (from 115 cm at the centre of the depression to 50 cm at the south-eastern margin of the mine). The first section contained the oldest ichnofossils (arthropod trackways), recorded 23 cm above the base of the grey claystones. In the next 20 cm interval, very many invertebrate traces (chiefly arthropods) were found at several levels. Swimming trails of fishes and amphibians occurred in the uppermost 30–35 cm. The other three sections studied exhibited a similar pattern of ichnofossil distribution. The swimming trails of fishes and amphibians appear together on some bedding planes, but fish traces are generally far more numerous. The oldest swimming traces, however, were made by amphibians. The preponderance of fish traces is undoubtedly associated with the much greater physical activity of fish. The striking decrease in arthropod traces is accounted for through their destruction by the movement of fish on the bottom; it may also be connected with feeding relationships. In the uppermost 15–20 cm, where swimming trails are most numerous, the rootlets of lycopodiophytes are common, both parallel with and oblique to the bedding. Immediately underlying the upper Radnice seam are grey clays, 16–40 cm thick, from which no fossils have so far been recovered.

The vast quantity of volcanic ash which accumulated on the floor of the flooded depression undoubtedly influenced fundamentally the chemistry of the water; the change could have been lethal for most of the inhabitants of the coal-swamp. Environmental conditions evidently stabilized during deposition of the upper claystones. The possibility that the observed succession of ichnofossils reflects a successive colonization of the lake – first by invertebrates, and then by vertebrates – cannot therefore be ruled out. The amphibian traces come mainly from the south-eastern edge of the exposure, where the depression was shallowest.

TAXONOMIC AND ETHOLOGICAL CLASSIFICATION OF ICHNOFOSSILS

Most of the invertebrate traces were made by arthropods; according to the ethological classification (cf. Frey and Seilacher 1980), only crawling traces (*Repichnia*) and resting traces (*Cubichnia*), are represented, together with fecal pellets. Fine, smooth, curving worm-like trails attributable to the ichnogenus *Haplotichnus* Miller, 1889, and problematical structures (ichnofossils?), morphologically similar to the genus *Paleoscia* Caster, 1942 (cf. Osgood 1970), were also found.

The vertebrate traces belong to the same ethological types as the invertebrate traces; coprolites are very rare. The amphibian traces document different behavioural types left by the same animal, and thus allow the application of biotaxonomic classification. They comprise resting traces, walking traces (footprints), and swimming trackways and trails, all produced by labyrinthodont amphibians of the order Temnospondyli (probably of the family Branchiosauridae or Dissorophidae). Standard palaeoichnological practice employs an ichnotaxonomic classification for different ethological types, which are defined by separate names (cf. Ekdale *et al.* 1984). It would thus be possible in some specimens (e.g. Pl. 74, figs. 1, 2) to define, in the course of a single trace, up to three separate taxa. Resting traces usually occur with another ethological type, or can be correlated with footprints; they are therefore not given a separate name. The footprints are very diverse but their morphological differences are related mainly to their mode of formation, and they are assigned to the single ichnospecies *Gracilichnium* (?) *chlupaci* ichnosp. nov. Of the swimming trails, two new ichnospecies are differentiated – *Lunichnium gracile* and *L. anceps*.

The morphological diversity of the fish swimming trails is considerable. Since there are intermediate forms between the individual types of traces, they have all been assigned to one new taxon – *Undichna radnicensis* ichnosp. nov.

Other common trace fossils (in the broad meaning of the term) are plant traces, represented in soft sediment by rootlets (penetration structures) of lycopodiophytes.

FISH TRACES

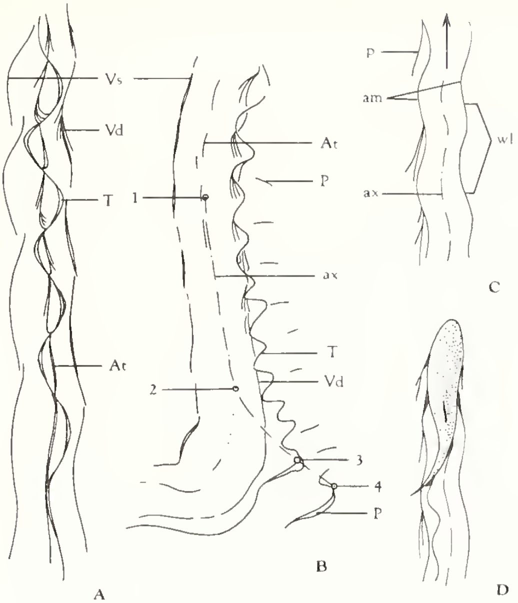
Apart from coprolites, fish leave few traces of their activity in the rock record – and then only benthic species living close to the bottom are represented. Resting traces are most common; these sometimes preserve a rough outline of the body, but are more often mere depressions that give little information about the appearance of the animal which made them (cf. Serjeant 1975). Among relevant studies of living fish, that by Schäfer (1962), based on observations of species in the North Sea, is especially important. Anderson (1976, p. 399) and Higgs (1988, pp. 271–272) have surveyed the most important studies on fossil fish traces.

Fossil fish traces have rarely been described. Especially interesting palaeoichnological material is known from the limnoglacial deposits of the Karoo Dwyka and Ecca Series of South Africa. These traces were first mentioned by Haughton (1925) and later interpreted by Abel (1935) as the swimming trails of stegocephalians. Jubb and Gardiner (1975), like Haughton, regarded them as the traces of acanthodians. Anderson (1970, 1976) documented their piscine origin in a detailed study. This South African material is especially important to any discussion of the new finds described herein, particularly as the described swimming trails made by recent fish show no close resemblances to Upper Palaeozoic traces.

Trace morphology. Most traces consist of just two marginal, subparallel, sinusoidal grooves (Vs and Vd), 12–30 mm apart and accentuated in alternate segments of the sinusoid (text-fig. 2). Along the axis of the trace (less often extramedially) there is quite frequently a discontinuous or continuous groove (At) which is out of phase with respect to the marginal grooves. A further sinusoidal groove (T), which displays a phase shift compared with the others and is characterized by its greater amplitude, lies inside the trace, but is not always in evidence; its marginal course often intersects the Vs or the Vd line. Exceptionally, in markedly asymmetrical traces, short, almost linear grooves (P) appear at regular intervals which equate roughly with the wavelength of the Vs and Vd lines, on the side nearer to the T line. They make an angle of 55–100° with the axis of the trace and are no more than 1 cm long.

Sometimes the undulating character of the trace is obscured by pronounced signs of sediment movement. The accentuated segments of the Vs and Vd lines may be directed obliquely backwards and change over to a large number of feathery grooves. The grooves (p) along the sides of the trace are sometimes the dominant morphological feature, when they may be distributed rather irregularly and of varying prominence and length.

While in general the traces usually follow an almost straight course, occasionally a sudden change of direction is evidenced and sometimes they may simply fade away (text-fig. 3).



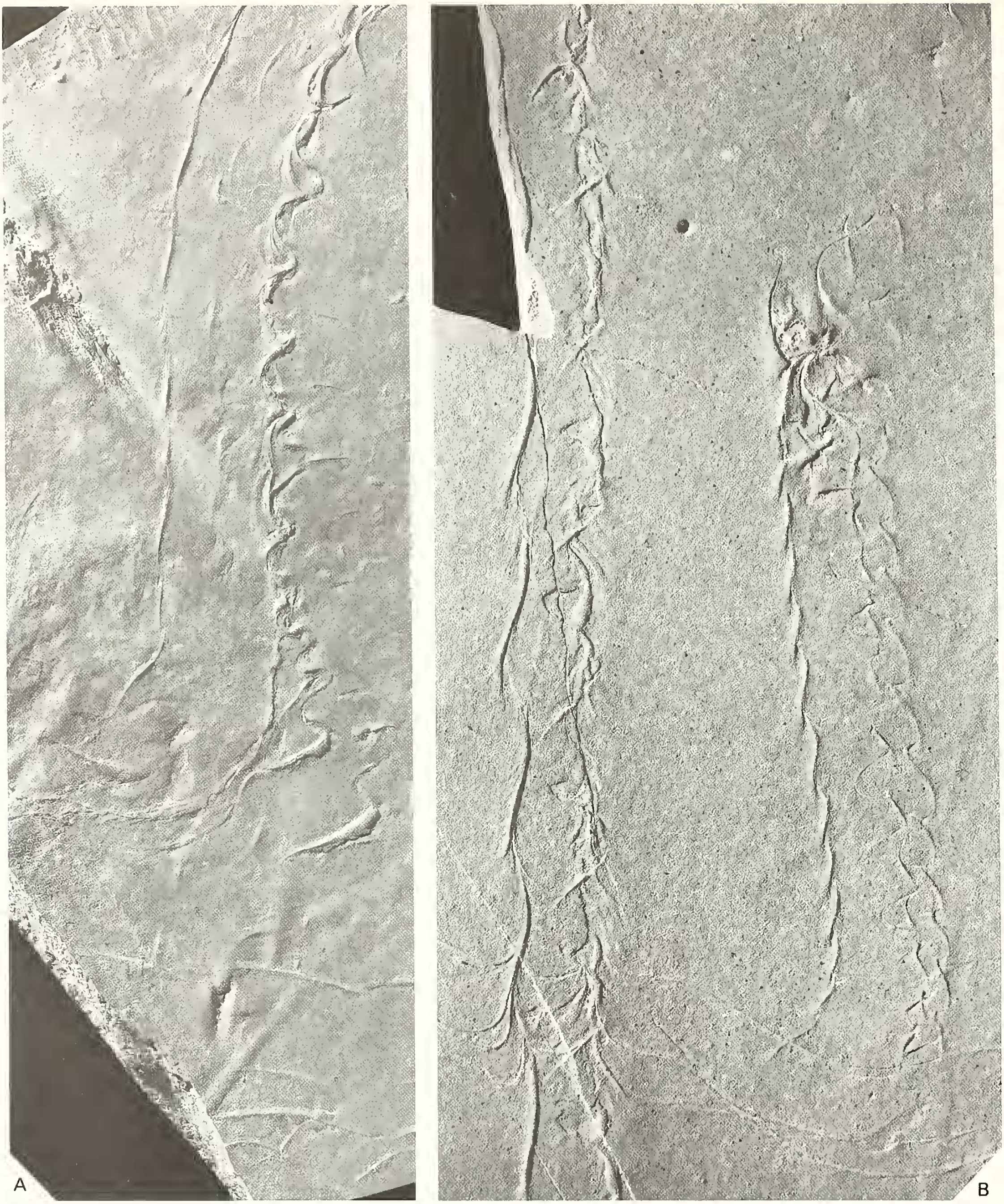
TEXT-FIG. 2. A–C, simplified drawings of fish swimming trails *Undichna radnicensis* ichnosp. nov., with an explanation of terms used in the paper and their morphological interpretation, based on: A, M 2089 (Pl. 73, fig. 2); B, M2092 (as used to estimate body length; text-fig. 3A); and C, M 2638. D, supposed origin of the fish swimming trail. Abbreviations: am, amplitude of marginal grooves; At, groove made by anal fin; ax, axis of trail; P and p, grooves left by pectoral fins; T, inner groove made by caudal fin; Vd, marginal groove made by right ventral fin; Vs, marginal groove made by left ventral fin; wl, wave length; 1, supposed position of head; 2, end of anal fin; 3, end of lower lobe of caudal fin; 4, end of upper lobe of caudal fin; arrow indicates direction of movement of trace maker.

Trace makers. The swimming trails give no indication of the taxonomic diversity of the living assemblage which made them. Their morphological similarity and the existence of intermediate forms suggest that, if the traces were left by several species, their representatives were both morphologically and ethologically similar. The makers of such swimming traces must have been either fish or amphibians, but the latter is less likely, for the following reasons: 1, the traces show no resting traces or footprints; 2, the morphology of the traces is consistent with a simple functional interpretation if we consider the possibility that they were made by fish (it is clear that they were formed by the edges of fins, and not by rigid outgrowths; see below); 3, from their general character, the traces must have been made by animals with a relatively high rate of physical activity; and 4, the present material is very similar to the swimming trails found in the Lower Permian of South Africa and the Upper Carboniferous of south-west England, and which were all interpreted as the traces of fish or acanthodians (Anderson 1970, 1976; Jubb and Gardiner 1975; Higgs 1988).

The main fish groups which merit consideration as potential trace makers are the Acanthodii and the Osteichthyes; both are well represented in the European Carboniferous. If acanthodians were responsible, then the width of some traces (over 30 mm) indicates a relatively large fish, with a total body length of more than 15 cm. This, however, is contradicted by the total body length estimated from the actual traces (see below). The indistinctness of the marginal Vs and Vd grooves as well as the single groove (At) shows that these marks were not made by spines, but by the flexible ends of fins (see Pl. 73, fig. 2). The trace makers were therefore more likely to have been Osteichthyes, and probably members of the subclass Actinopterygii (with a heterocercal caudal fin) – and which are indeed the most common fish in the Upper Carboniferous of Bohemia.

The traces enable some conclusions to be drawn concerning the gross morphology of their makers. The fish had a typical piscine body, i.e. torpedo-shaped. All the fins were 'normal' in length, so that when swimming close to the bottom, the lower lobe of the heterocercal caudal fin, the distal end of the anal fin, and the ends of the ventral fins might contact the substrate. The traces left by the pectoral fins (especially where the animal suddenly changed direction; text-fig. 3A) suggest that they were relatively long, and that their length probably exceeded the width of the body.

In estimating the length of the fish's body from the traces available, Bainbridge's (1958, 1963) observations of recent teleostomes were taken into account. He observed that the amplitude of the caudal fin was not more than one fifth of body length, and also that, above a certain minimum



TEXT-FIG. 3. *Undichna radnicensis* ichnosp. nov., Type A. Fish swimming trails. A, M 2092 (see text-fig. 2B), strongly asymmetrical trail exhibiting sudden change of direction; in the lower part of the picture there is a segment of another strongly asymmetrical trail, × 0·8. B, M 2079, two trails crossing an earlier one; note the sudden appearance and disappearance of the right-hand trail, × 1.

TEXT-FIG. 4. *Undichna radnicensis* ichnosp. nov. Fish swimming trails, M 2638. Two trails of opposite orientation crossing an earlier one. Both vertically oriented trails possess a well-expressed groove p (outside the sinuous marginal grooves Vs and Vd). The trail on the right is transitional between Type A and Type B, ×0·7.

swimming speed, there were usually about 1·6 wavelengths down the length of a fish. Another possibility considered was whether body length could be estimated from the highly asymmetrical traces and from one trace showing a sudden change in swimming direction (M2092; text-figs. 2B, 3A). Here the approximate distance between the end of the lower lobe of the caudal fin and the anal fin could be usefully measured since, despite marked differences even among the various Carboniferous species, this distance generally correponds to between one-quarter and one-fifth of total body length. To determine the absolute distance between simultaneous traces of caudal and anal fins, the direction of movement and the presumed curvature of the caudal part of the body must be taken into account. Further information about size was obtained from M2092 by comparing it with the path of the head and tail of a living rudd turning through a right-angle (as illustrated by Gray 1968, p. 78, fig. 4.9A). From the above considerations, it appears that the total body length of the trace makers varied between 5 and 12 cm. These morphological data, together with what is known about actinopterygians from the Upper Carboniferous of Bohemia (Zajíc and Štamberg 1986), indicate that the trace makers probably belonged to the order Palaeonisciformes. From such contending actinopterygian genera as *Pyritocephalus*, *Sceletophorus*, and *Sphaerolepsis* (all established by Fritsch 1879–1901), the last deserves particular consideration due to its morphology and dimensions, although it remains unknown before the Stephanian.

Functional interpretation. The marginal Vs and Vd grooves, which are always discernible, were probably made by the ends of the ventral fins. In some exceptional cases the sediment was thrown up in furrows or very fine grooves that point obliquely backwards beyond the trace (p) and which were probably made by slightly spread pectoral fins (Plate 73; text-figs. 1, 4). The short, laterally oriented grooves that occasionally appear on one side of the trace (P) are also considered to have been made by a pectoral fin. The single groove along the axis of the trail (At) was left by the anal fin. The inner groove with the greatest amplitude (T) was undoubtedly made by the distal end of the lower lobe of the caudal fin.

The variety of traces is considerable and is evidently a function of the trace maker's proximity to the lake bed, its rate of locomotion, and movement of the fins, etc. In some particularly pronounced traces, distinguished by the sediment having been thrown markedly sideways, the characteristic undulating character of the trace is largely obliterated.

Determination of swimming direction. In swimming trails, the direction of movement can, in most cases, be determined unequivocally. Where traces intersect, as the sediment was churned up, earlier traces were lifted and 'blended' with the later traces (text-figs. 3B, 4). A secondary change in the course of the older trace, or the direction of deflection in places where it was intersected by a later trace, show the direction of the animal's movement. In isolated traces, the most pronounced segments of the Vs and Vd grooves diverge slightly obliquely backwards, beyond the sinusoidal line reflecting the undulatory body movement. In some cases, these grooves are accompanied by other, less conspicuous grooves. Fine feathery grooves may also accompany the trace of the anal fin (At), if its distal end was in close contact with the substrate (text-fig. 2A; Pl. 73, fig. 2).

Ethological conclusions. The type of locomotion of the trace-making fish was similar to that of recent teleostomes, in which 'during steady fairly fast locomotion, forward progression is effected entirely by lateral movement of the body and caudal fin' (Bainbridge 1963, p. 25). The amplitude of lateral movement increased in a craniocaudal direction.

The traces are often strikingly asymmetrical, as manifested chiefly in a lateral shift of the groove made by the caudal fin and by differences in the course of the marginal grooves. This course may have been due, at least in part, to asymmetrical movements of the caudal fin, i.e. to an inequality in the rate of transverse movement of the end of the caudal fin in relation to the axis of locomotion. This type of asymmetrical movement is common among recent teleostomes 'and appears to be normal during steady swimming and perhaps during slowing. Also, more gentle turning can be effected, however, by asymmetrical tail movement, the pectoral fins remaining pressed to the body' (Bainbridge 1963, pp. 35–36). The groove made by the anal fin can also follow a course that diverges markedly from the axis of the trace as a whole. The general character of the traces (e.g. sudden changes of direction, sedimentary structures formed by churning movements of the body, the lifting of older traces intersected by later traces, etc.) is indicative of an active animal with a laterally very flexible body, and capable of sudden changes of direction and speed.

From the size of the traces, it appears that the early growth stages of the fish lived some distance above the lake bed, and therefore left no record of their existence in the sediment. Except at such young stages of development, the fish may well have eaten the amphibians and arthropods whose traces occur in association with their own.

EXPLANATION OF PLATE 73

Figs. 1–3. *Undichna radicensis* ichnosp. nov. Fish swimming trails. 1, M 2097, Type B; section of trail with partial exfoliation of clay laminae; oblique, posteriorly directed grooves (p) predominate; inside the trail, sinuous groove (T) is visible, ×0·7. 2, M 2089, holotype, Type A (see text-fig. 2A); almost symmetrical, undulating trail demonstrating variable contact of fish with substrate, variable speed of trace maker, and flexibility of distal end of anal fin (see upper third of picture), ×0·7. 3, M 2094; part of strongly asymmetrical trail, with short isolated grooves (P) almost perpendicular to midline of trail, ×0·8.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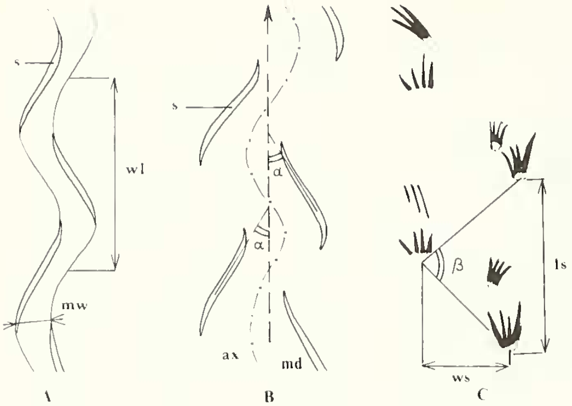
2


3

TUREK, *Undichna*



TEXT-FIG. 5. Simplified drawings of amphibian traces, with an explanation of terms used in this paper. A, swimming trail. B, swimming trackway. C, walking traces. Abbreviations: α, angle between segment and midline of trace; β, step angle (pace angle); ax, axis of trace; ls, length of stride; md, midline of trace; mw, maximum width of trace (in amplitude); s, well expressed segment of sinusoid; wl, wave length; ws, width of stride; arrow indicates direction of movement of trace maker.

AMPHIBIAN TRACES

Among the many traces of tetrapods described from the Upper Palaeozoic of Europe, only a small proportion is of Late Carboniferous age. Actualistic studies, like those of Peabody (1959) and Fichter (1982, 1983), are of fundamental significance for the taxonomic evaluation of tetrapod trace fossils. Most palaeontologists, however, have concentrated their attention on walking tracks and the evaluation of footprints, and have rarely mentioned swimming trails (e.g. Schmitgen 1928; Abel 1935; Müller 1955; Hoeningen-Huene 1960; Boy and Fichter 1982; Haubold 1982; Walter 1982). Some of these finds have not yet been assigned with certainty to any particular vertebrate group. The possibility of correlating individual ethological types is, as a rule, very limited. It is this aspect of the material described herein which is especially remarkable.

Morphology of swimming trails and trackways. The swimming *trail* is a continuous sinusoidal trace bounded on both sides by a marginal groove of unequal depth, alternately widening and duplicated at regular intervals. The traces are 3–12 mm wide. Greatest separation of the marginal grooves is at maximum amplitude (text-fig. 5).

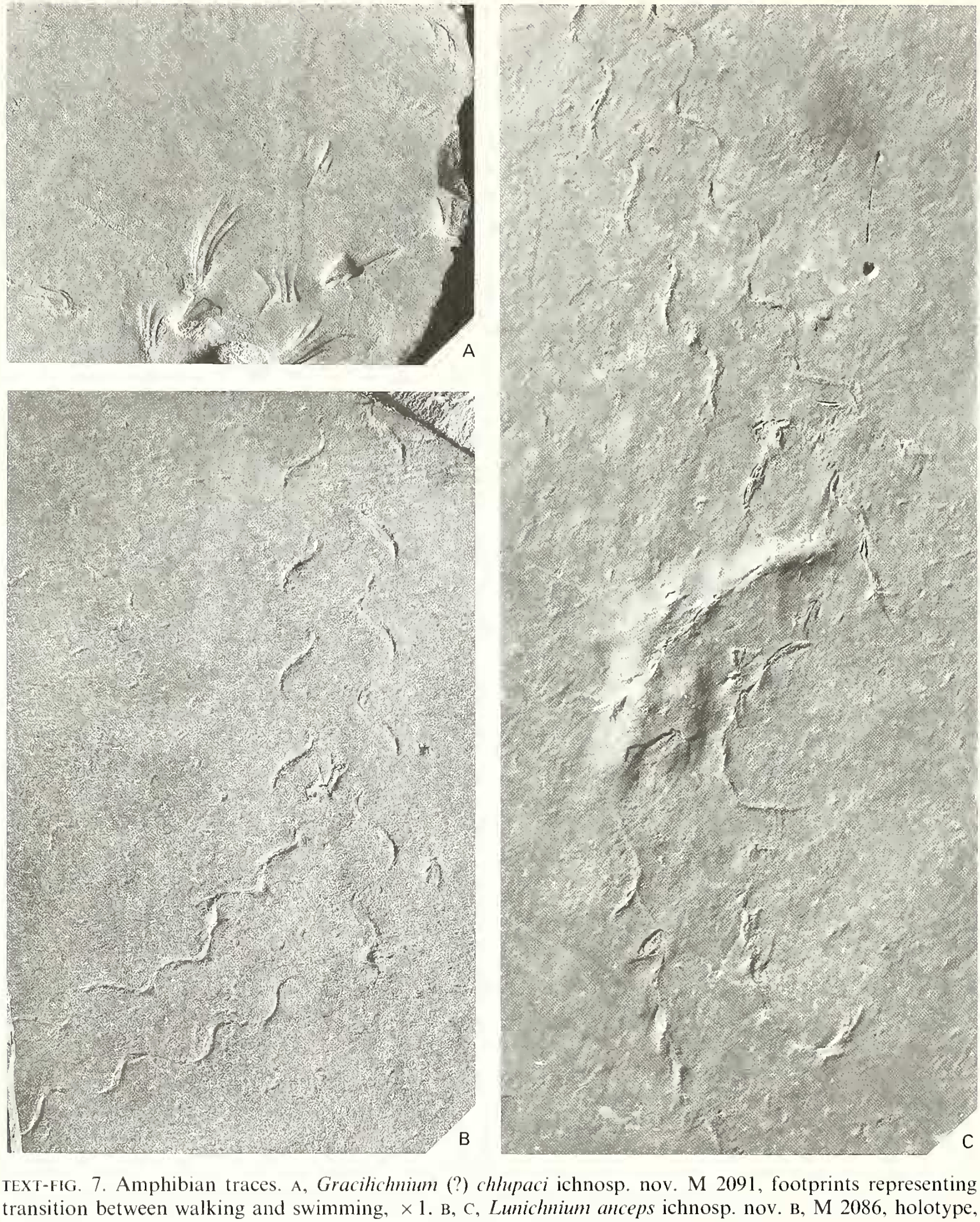
The swimming *trackway* is a discontinuous trace consisting of faintly S-shaped, twin and reconverging grooves situated alternately on either side of the axis of the trace and forming an angle of *c.* 15–45° with the axis denoting the direction of locomotion. The individual S-shaped elements are 8–20 mm long (text-figs. 6, 7).

Both types of trace often change over from one to the other without a break, and they are usually almost straight. As a rule, resting traces appear after 20–40 cm. Before the sinusoidal trail or trackway reaches a resting trace, it widens (or even disappears), traces of limbs (one pair or two) appear, and the space between the marginal grooves is usually no longer differentiated. In exceptional cases (text-fig. 6B), a short, curved, rapidly widening and fading trace, with a distinct phase shift in relation to the marginal grooves, leads from the axis of the trace.

Morphology of walking traces (footprints). Footprints occur most frequently at resting places, or they mark a brief interval of locomotion across the substrate; they are usually associated with swimming trails. Footprints of individual traces may show considerable morphological variation, for two reasons. First, all the traces were made under water; where the amphibian trod, it sometimes slipped, so that the resulting footprints do not exactly match the contours of the manus and the pes. Secondly, as a result of buoyancy, the feet did not need to support the full weight of the amphibian; like living newts, it touched the bottom only with the tips of the digits, or stood on only one or two feet.

For the ichnotaxonomic classification of such traces, a trackway of footprints (composed of at

TEXT-FIG. 6. *Lunichnium gracile* ichnosp. nov. Amphibian swimming trails. A, M 2085, holotype, trail interrupted by resting traces with impressions of forefeet, ×0·8. B, M 2088, short, narrowly sphenoidal curved traces with a groove along the axis of the trail made by the tail, ×0·7. C, M 2082, trackway crossing continuous trail, ×0·8.



TEXT-FIG. 7. Amphibian traces. A, *Gracilichnium* (?) *chlupaci* ichnosp. nov. M 2091, footprints representing transition between walking and swimming, ×1. B, C, *Lunichnium anceps* ichnosp. nov. B, M 2086, holotype, ×0·8; C, M 2083, ×0·9; swimming trails showing changes in direction with impressions of feet.

TEXT-FIG. 8. *Lunichnium gracile* ichnosp. nov. and *Gracilichnium* (?) *chlupaci* ichnosp. nov. M 2080, schematic drawing of Pl. 74, figs. 1 and 2, with tentative outline of the trace maker.

least three sequential sets of impressions) must be preserved (Serjeant 1975). The only specimen here that approaches this condition is M 2084 (Pl. 75, fig. 1), except that it is an intermediate trace between walking and swimming. The small impressions of the manus and the pes are arranged fairly regularly. Along one side of the trace the manus and the pes are not completely aligned and their axes are distinctly offset relative to each other. The manus has four digits and of the five digits of the pes, only four are discernible. The length of the stride of the hind limbs corresponds to double the width of the step, which has an angle of 90°. The digits are very thin and sharply-tipped, and are closer together on the fore limb than on the hind limb.

Morphology of resting traces. These are generally preserved in association with swimming trails. Each represents a halt made by the animal before swimming again. Here the trace maker left more or less distinct impressions of its limbs (text-fig. 6A; Pl. 74, figs. 3, 4), or else its whole body rested on the bed, leaving an impression of its ventral surface and limbs on the sediment surface (Pl. 74, fig. 2).

The trace makers. All stages of amphibian growth are represented by the traces studied, except the early larval stages. My reconstruction of the trace maker is based primarily on a unique resting trace (Pl. 74, fig. 2; text-fig. 8) which was evidently made by an adult, 60–70 mm long, with a wide, semicircular skull 16–17 mm long and 23 mm wide at the caudal end; the relatively short tail measured about 25 mm. Since it did not, as a rule, leave any trace, it can also be assumed that the sexual dimorphism known in recent urodeles, which is manifested, *inter alia*, in the shape and size of the tail, was not sufficiently expressed. The fore limb had four digits and the hind limb five; the digits were very thin and had pointed tips.

From these morphological characters and the stratigraphic age of the finds, it is considered that the maker of the traces is a member of the order Temnospondyli, family Branchiosauridae (e.g. *Branchiosaurus*) or Dissorophidae (*Amphibamus*) (Boy 1972, 1978; Milner 1974, 1982, 1986), which are represented fairly abundantly in the Permo-Carboniferous of Bohemia.

Functional interpretation. The swimming traces show the undulations of the animal's body during this type of locomotion. The amphibian left either swimming trails or trackways, according to the closeness of its contact with the substrate. The traces on the bottom were made by the distal ends of the longest digits (III and IV) of the hind limb, which (like the fore limbs) the swimming animal held stretched out backwards. A similar swimming technique is employed by living newts. The relatively short tail was not in contact with the substrate during swimming, and thus generally left no trace. Before reaching the resting trace, the swimming trace widens because the limbs were drawn away from the body.

Determination of the direction of movement. The direction of locomotion in amphibian swimming trackways is indicated by the orientation of the acute angle formed between the isolated, slightly S-shaped furrows and the midline of the trace. In swimming trails it is indicated by the acute angle formed between the accentuated segments of the sinusoidal trace and the midline. The direction of locomotion can also be determined from isolated S-shaped elements, whose curvature is anteriorly greater, and the end of the trail more sharply pointed, than at the posterior end.

Ethological conclusions. Along the course of the traces – even the narrowest – places where the animal rested on the substrate can often be found, leaving distinct impressions of fully developed limbs. All the traces probably therefore belong to the different growth stages associated with metamorphosis. Finds of isolated footprints completely unassociated with swimming trails show that the animal was not confined to the bottom. The orientation of the digits of the fore and hind limbs in the resting traces is very varied, but the digits of the manus usually point forwards and obliquely sideways, while the hind limb digits are oriented obliquely backwards. The behaviour of these ancient amphibians does not seem to have differed significantly from the behaviour of living newts, of which the male and female sharp-ribbed Salamander (*Pleurodeles waltl*) were observed for comparison. Judging by their similarity to living amphibians, the trace makers were probably carnivorous too, living chiefly on arthropods.

SYSTEMATIC PALAEONTOLOGY

All the material discussed was collected from the Radnice Member of the Kladno Formation (Westphalian C, Upper Carboniferous) in the open-cast coal mine at Přívětice-Ovčín, (Radnice Basin, western Bohemia,

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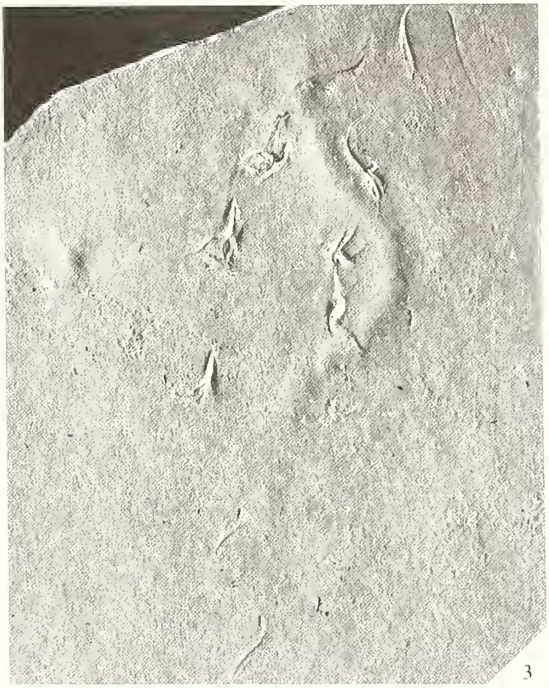
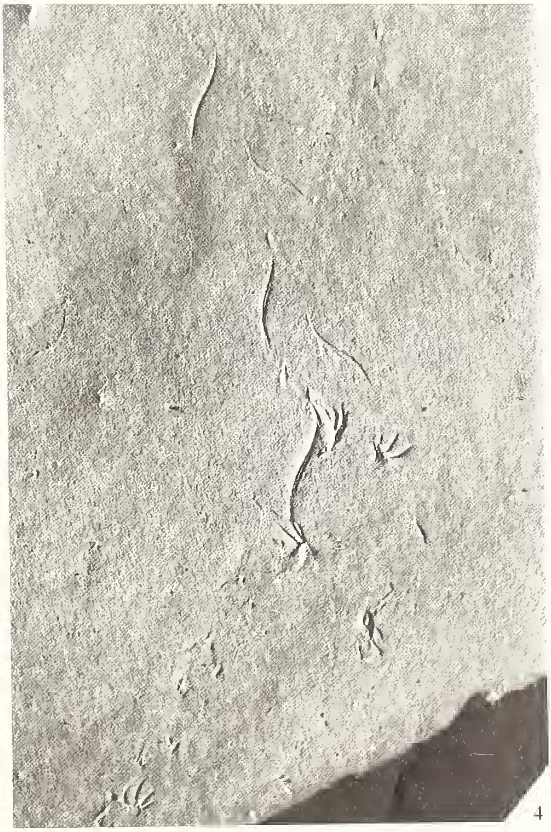
EXPLANATION OF PLATE 74

Figs. 1–4. *Lunichnium gracile* ichnosp. nov. and *Gracilichnium* (?) *chlupaci* ichnosp. nov. Amphibian swimming, walking, and resting traces. 1, 2, M 2080 (see text-fig. 8), two parts of one trace, × 0·9. 3, 4, M 2090, two parts of one trace; swimming trail interspersed with resting traces; walking trackway appears at bottom of fig. 4, where only distal ends of digits were in contact with substrate, × 1.


1


3


2


4

TUREK, *Lunichnium*, *Gracilichnium* (?)

Czechoslovakia); it has been deposited in the Palaeontology Department of the National Museum, Prague. All photographs in this paper show hyporelief; the explanations, however, relate to epirelief. The traces are oriented as though the trace maker moved across the page from bottom to top. Photographs were produced by K. Drábek and V. Turek.

Genus UNDICHNA Anderson, 1976

Type species. Undichna simplicitas Anderson, 1976, from the Dwyka Series (Lower Permian) of Swart Umfolozi, South Africa.

Diagnosis. See emended diagnosis of Higgs (1988, p. 257).

Discussion. Trace fossils assigned to *Undichna* have been found in the Great Karroo basin, South Africa, in fresh water sediments of Late Permian age, Queensland (Warren 1972), in the Pennsylvanian of Indiana (Archer and Maples 1984), and in the Upper Carboniferous of south-west England (Higgs 1988). The specimen from Žebrák-Na Štýlci, Central Bohemia, figured by Walter (1982, pl. 2, fig. 4), and probably also his pl. 2, fig. 2, can be reassigned similarly. Both were interpreted by Walter (with some doubt) as arthropod swimming trails. Stratigraphically, these trails correlate with those from the Radnice Basin.

Undichna radnicensis ichnosp. nov.

Plate 73; text-figs. 2–4

Holotype. M 2089 (Pl. 73, fig. 2).

Material. More than forty specimens, some of them with several trails, all registered under PM2 4/87.

Derivation of name. After the Radnice Member.

Description (for abbreviations see text-fig. 2). Undulating trail bounded by two marginal subparallel sinusoidal grooves (Vs and Vd) that display a regularly alternating pattern in their degree of expression. Trace width ranges from 12 to 30 mm. The posterior portion of the more expressed segments is sometimes elongated backwards (i.e. outside the wave). Down the axis of the trail, or eccentrically, there is another continuous or discontinuous groove (At), out of phase with the marginal grooves. Besides this groove, inside the trail, or more frequently near one side of the trace, there is a sinusoidal groove (T) of greater amplitude that displays a phase shift compared with the others. Occasionally, in highly asymmetrical traces, short grooves appear outside the trail at regular intervals, oriented obliquely (p) to perpendicular (P) to the course of the trail.

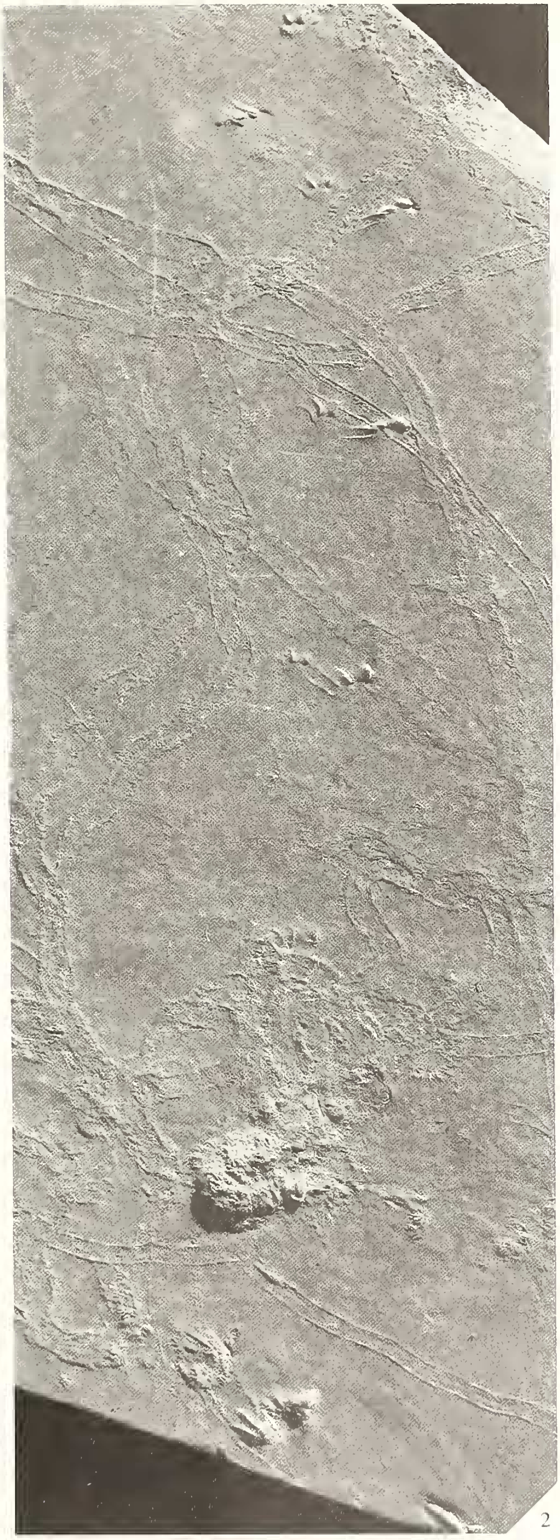
Discussion. U. radnicensis ichnosp. nov. is highly variable in morphology. It can resemble *U. britannica* Higgs, 1988, when certain characteristic features are lacking, but the marginal grooves in the British species are discontinuous and rarely visible. If only two sinusoidal grooves are present, they are not so clear-cut, equally developed at a constant distance apart as in *U. bina* Anderson, 1976.

Two morphological types of trail (A and B) can be distinguished but, since transitions between them exist, two ichnospecies have not been established. Both types of trace could have been produced by the same animal moving at different speeds and with pectoral fins in a different position.

Type A trails (Pl. 73, figs 2, 3; text-figs. 2A–C, 3, 4) show a clearly expressed undulating course. Their marginal grooves are sinuous, and when they occur in connection with other grooves directed obliquely backwards, the latter are short and poorly developed.

EXPLANATION OF PLATE 75

Figs. 1, 2. *Lunichnium gracile* ichnosp. nov. and *Gracilichnium* (?) *chlupaci* ichnosp. nov. Amphibian swimming and walking traces. 1, M 2084, holotype of *G.* (?) *chlupaci*, ×0·9. 2, M 2081, showing transition between walking and swimming; the impressions correspond to footprints of only one side of the animal, × 1.



TUREK, *Lunichnium*, *Gracilichnium* (?)

Type B trails (Pl. 73, fig. 1) follow an indistinct undulating course. Their predominant morphological features are long grooves directed obliquely backwards and often terminally branching. These grooves are often accompanied by fine furrows showing the same orientation. Type B trails have a more distinct relief than Type A trails. Owing to the partial exfoliation of claystone laminae, the preservation of Type B trails is not very good and other morphological features are not clearly expressed; none shows a medial groove left by the anal fin.

Both types of trail are interpreted as the swimming trails of fishes of the subclass Actinopterygii, order Palaeonisciformes. The morphology of *Sphaerolepis* Fritsch seems to be a good match for the described trails.

Genus LUNICHNIUM Walter, 1983

Type species. Lunichnium rotterodium Walter, 1983, from the Rotteröder Member at Rotteröde, Thuringia, German Democratic Republic.

Diagnosis (supplemented herein). Sinuous trail bounded by a pair of sinusoidal grooves with a regularly varying separation; the greatest separation occurs at maximum amplitude. These grooves are widened and bifurcated in alternate segments of the sinusoid (Type A). Frequently only the widened and more expressed parts of the sinusoid are preserved, and the trace then consists of isolated elements. Paired sets of slightly to moderately S-shaped elements bifurcate and reconverge, forming an acute angle with the midline of the trace (Type B). Type A may pass gradually into Type B, even in the same trace.

Discussion. Lunichnium was established on a discontinuous trackway of Type B morphology, as defined here, which also exhibits some irregularities (Walter 1983, pl. 8, fig. 7; pl. 9, fig. 1). Thus, short paired furrows appear on the right-hand side of the trackway in the lower and upper parts of Walter's illustrations. These impressions may be interpreted as traces left by the forefeet which were held at a greater distance from the body during less continuous movement. An unnamed trail from the Oberhöfer Member at Neues Haus, figured by Walter (1983, fig. 4*b*; pl. 10, fig. 4), may be identified with the trails assigned to *Lunichnium* Type A.

Single-row traces of *Servichnus* (Holub and Kozur 1981, pl. 14, figs. 1, 2) may be compared with *Lunichnium* Type B but, apart from having only one row of elongated, bifurcated, and reconvergent grooves, the traces included within *Servichnus* differ in having additional minute, shortly elongated impressions. In addition, the grooves do not show the typical S-shape (both ends deflected to the same side) (cf. Holub and Kozur 1981, fig. 2B).

Lunichnium Type A resembles the invertebrate trail *Cochlichnus* Hitchcock, 1858, which has been interpreted as the crawling traces and probable feeding structures of a small worm or worm-like animal (Eagar *et al.* 1985). The width of a *Cochlichnus* trail is less than 5 mm. It may be preserved as a winding to sinuous convex or concave epirelief, and lacks the conspicuous widening in amplitude and the bifurcating alternating elements, on both sides of the trail, that characterize *Lunichnium* Type A.

Lunichnium gracile ichnosp. nov.

Plates 74 and 75; text-figs. 6 and 8

Holotype. M 2085 (text-fig. 6A).

Material. Thirteen specimens, some with several traces, all registered as PM2 4/87.

Diagnosis. Lunichnium characterized by a narrow trace (4–5 mm). Wave length ranges from 10 to 35 mm.

Discussion. The unnamed trail figured by Walter (1983, fig. 4*b*; pl. 10, fig. 4) can be assigned to this ichnospecies.

Lunichnium anceps ichnosp. nov.

Text-fig. 7B,C

Holotype. M 2086 (text-fig. 7B).

Material. Five trails and trackways, all registered as PM2 4/87.

Diagnosis. *Lunichnium* characterized by a wide trace (10–14 mm). Wave length ranges from 12 to 16 mm.

Genus GRACILICHNIUM Haubold, 1970

Type species. *Gracilichnium jacobii* Haubold, 1970, from the Goldlauterer Member (Lower Permian) at Friedrichrodà, Thuringia, German Democratic Republic.

Diagnosis. See Haubold (1970).

Gracilichnium (?) *chlupaci* ichnosp. nov.

Plates 74 and 75; text-figs. 7A and 8

Holotype. M 2084 (Pl. 75, fig. 1).

Material. Four trackways and several other specimens showing footprints, all registered as PM2 4/87.

Derivation of name. In honour of Dr I. Chlupáč, an outstanding Czech geologist and palaeontologist.

Diagnosis. A small amphibian trackway with rather regularly arranged impressions of four-toed forefoot (manus) and five-toed hindfoot (pes). The footprints of manus and pes on the same side are not in line, their axis being slightly off-set. The length of stride determined from the impressions of the hindfeet corresponds to twice the width of the stride. The pace angle is 90°. The digits are very thin and pointed, slightly curved, and less divergent in the manus than in the pes.

Discussion. This taxon is based mainly on the holotype. Additional specimens of footprints from the Přívětice-Ovčín locality are thought to belong to the same ichnospecies, although direct evidence for conspecificity is lacking. These footprints are preserved on resting places or in trackways, where only the distal ends of digits were in contact with the substrate. The holotype is itself a trackway representing a transition between walking and swimming. For this reason, the traces described in this paper are hardly comparable with typical walking traces. The impression of the sole is usually missing, or is only slightly expressed. In addition, the true length of the digits is often indeterminable because of the sliding gait.

Lunichnium and *Gracilichnium* (?) from the Radnice basin are interpreted as the swimming and walking traces of labyrinthodont amphibians, of the order Temnospondyli (probably branchiosaurids or dissorophids, like *Branchiosaurus* or *Amphibamus*).

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